ON THE
LIFE-HISTORY AND DEVELOPMENT
OF THE
GENUS MYZOSTOMA (F. S. LEUCKART).

INAUGURAL-DISSERTATION

FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

PRESENTED TO THE

HIGH PHILOSOPHICAL FACULTY

OF THE

UNIVERSITY OF FREIBURG I/B.

BY

JOHN BEARD
OF MANCHESTER.

LEIPZIG
WILHELM ENGELMANN
1884.

(Separatabdruck aus »Mittheilungen a. d. Zoolog. Station zu Neapel.« V. Band.)

On the Life-History and Development of the Genus Myzostoma (F. S. Leuckart).

Historical Introduction.

The genus *Myzostoma* has from the time of its first discovery been one of the most doubtful genera among the *Invertebrata*. Of the anatomy we have in past years learnt much, especially by the researches of SEMPER[1] and GRAFF[2]. But the embryology, which as is well known usually gives good criteria for determining the position of a group, was almost unknown to previous observers.

The first stage in the development recorded, was an advanced one observed by SEMPER[3]. It had a simple, unbranched alimentary canal and two pairs of legs. The discovery of this larva was of no importance for determining the systematic position of the group. Indeed it taught very little, and led rather to erroneous comparisons with the *Nauplius* larva of *Crustacea*. In 1866 METSCHNIKOFF[4] described accurately the segmentation of the egg of *M. cirriferum*, and figured a ciliated larva of a simple form — little more than a planula.

He further described some of the later stages in which the larva is already in possession of its host. In both these cases the larva has permanent legs, in the one case two pairs, in the other the full complement of five. Both had a proboscis, and simple unbranched alimentary canal. But although METSCHNIKOFF's paper contained the description of a not

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[1] SEMPER, Zur Anatomie und Entwicklungsgeschichte der Gattung *Myzostoma* (Leuckart). Zeitschr. f. wiss. Zool. Bd. IX. p. 48—64. Taf. III u. IV.

[2] GRAFF, Das Genus *Myzostoma*. Leipzig 1877.

[3] l. c. p. 60.

[4] METSCHNIKOFF, Zur Entwicklungsgeschichte von *Myzostomum*. Zeitschr. f. wiss. Zool. Bd. IX. p. 236—243. Taf. XIII A.

inconsiderable course of development, it does not include the whole, nor even the most important part of the larval history. This was no doubt due to the smallness of the larvae to be dealt with, and the non-success of all efforts to obtain artificial fecundation. This bad fortune METSCHNIKOFF shared with SEMPER and GRAFF, neither of whom were able to obtain results in this direction. In his monograph of the genus GRAFF added but little to our knowledge of the development of the genus; the whole of his results under this head being contained in the following[1]: »Und so sind es nur die Entwicklungszustände von 0,2 mm Länge an, welche ich kenne. Doch gestatten auch diese einen kleinen Fortschritt in der Erkenntnis der Entwicklungszustände unserer Thiere. Larven von dieser Länge zeigen 3 bis 5 Fußpaare, terminalen Mund und After, einen wohl ausgebildeten Bulbus musculosus und einfachen unverästelten Magen.«

I have had more good fortune in attempting to bridge over the gap in our knowledge of the development, and have further been successful in obtaining artificial fecundation, to which success, no doubt, no inconsiderable portion of the results obtained is due.

Such briefly was the state of our knowledge of the embryology of the group, when at the close of last year I began my researches. We knew the segmentation fairly well by METSCHNIKOFF's researches, and we knew that a completely ciliated larva left the egg. But beyond this point the larval history was totally unknown. Of the post-larval history a fair proportion was known from the researches of SEMPER, METSCHNIKOFF and GRAFF, but this knowledge does not seem to have been enough to determine even approximately the systematic position of the genus. METSCHNIKOFF, it is true, with his usual perspicuity, was lead by his researches to class the *Myzostomidae* among the *Chaetopoda*, and indeed, as a special division *Chaetopoda parasitica*; but while the views of this distinguished zoologist were adopted by many others, including CLAUS in his Grundzüge der Zoologie[2], Prof. GRAFF in his Monograph and later papers on the group regarded the genus as allied to the *Tardigrada* and *Linguatulidae*. With what justification we shall see in the sequel.

Methods of research.

A few words on the methods employed may perhaps not be out of place. The development was mainly studied on the living animal. Con-

[1] l. c. p. 66. [2] Vierte Auflage. 1880. p. 506.

served material in whatever way prepared yielded but little result. Larvae were prepared in all sorts of ways for microscopic examination, mounted whole and in sections. But the usual result was disappointment. Hence the drawings of the development given are mostly from the living object, and only in the case of two are sections figured. The above applies only to the segmentation and true larval stages.

My earlier attempts to effect artificial fecundation were, like those of my predecessors, without result. And so in the earlier portion of the research larvae had to be sought with great trouble, and in few numbers in the glasses of sea-water in which *Comatulae* with *Myzostomidae* had been placed. This was a very troublesome and tedious proceeding especially as it was impossible to keep the *Comatulae* alive in small glasses for any length of time. Still it was not uncrowned with success, for it yielded a tolerably complete picture of the whole course of development, which served to control and verify the later researches on segmenting eggs and larvae obtained by artificial fecundation. To obtain naturally fertilised eggs the following method, provided *Comatulae* are very abundantly to be had, yields very fair results. A number of *Comatulae* infested with large full grown *M. glabrum* are taken, and the arms cut away not far from the disc. The *Comatulae* with their *Myzostomidae* are then placed in small deep glasses filled with sea-water, and a gentle current of sea-water is allowed to flow thro' the upper part of the glass. Eggs are laid pretty nearly every day, if not every day, and as these eggs are specifically heavier than sea-water, they sink to the bottom. If after one day the *Comatulae* be placed in a fresh glass, the water in the first glass will contain a number of segmenting eggs or larvae the age of which is approximately known. These may be kept living 4 or 5 days or even more, and examined at any stage. But by this method the eggs obtained are not very numerous, and after the *Comatulae* have been in the glasses a few days they usually break up, and then the parasites die.

Whenever it was desired to examine the larvae contained in a glass, in the case of both naturally and artificially fertilised eggs, the water was filtered down to a small bulk. In this way a number of larvae could be obtained in a very small quantity of water at the bottom of the filter.

This laborious method of obtaining larvae was superseded in the later portion of the work by the discovery of an easy method of obtaining artificial fecundation. A number of full sized *Myzostomidae* are removed carefully from their hosts, and placed in a small shallow glass,

such as a watch-glass, along with about two or three teaspoonfuls of freshly filtered seawater; the animals are then well teased with clean needles, so that a great number of eggs and spermatozoa are obtained in the seawater. The mixture of pieces of *Myzostomidae* is well stirred up and allowed to stand for two or three hours. Then the pieces of *Myzostomidae* are picked out with needles, and the water with its contained eggs thrown into a glass full of freshly filtered seawater. This glass is covered, and placed under the ANDRES air-apparatus, by which means a gentle current of air can be passed through it, and the water kept well aërated.

Development then goes on and the larvae may be examined at any stage. It is easy to get them to develop for five or six days, but beyond that the usual well-known result ensues — most of the larvae die. It is well to renew the seawater every second or third day. This is easily effected. The minute larvae always remain at the bottom, and thus allow of the pouring away of the greater portion of the water, and so of its renewal.

It is necessary to take at least four or five *Myzostomidae* in each experiment, for as the animals are hermaphrodite, self-fertilisation must be as far as possible avoided. The number of instances in which it can occur is, of course, very much diminished by increasing the number of individual *Myzostomidae* used in each experiment.

For the investigation of the later stages of the development — that is of the post-larval stages — the *Comatulae* were slowly killed in the well-known mixture of alcohol and seawater. The *Comatulae* were placed in a vessel containing a mixture of seawater with ten per cent Alcohol. When dead they were individually seized with forceps, and well shaken in the mixture. The small *Myzostomidae* of both species, and also the full grown *M. cirriferum* are thus shaken off in great numbers, and fall to the bottom. The superabundant water is poured off, and alcohol is gradually added until the animals lie in 90 % Alcohol. A great number may be then stained together and mounted for microscopic examination.

In the following portion of the work I have divided my subject under three heads, viz. Anatomy, Development, and section on the males of *M. glabrum*.

Anatomy and Histology.

Although it is not my intention to enter fully into the anatomy and histology of the adult, nor indeed is such a task necessary, for SEMPER[1] and GRAFF[2] have both studied it with great exactness and detail, still there are some points in which I am able to add to our knowledge under this head. These chiefly concern the nervous system, sense organs, and alimentary canal.

Skin and Sense organs.

As is already well known the skin of *Myzostoma* is made up of a cuticle underlying which is a layer of cylindrical ciliated epithelium. This cylindrical epithelium is composed of cells the bases of which do not rest on a basement membrane, but are prolonged into processes which stretch into the sublying cutis (fig. 32).

Whether they are there connected with nerve ganglion cells or not, as Flemming has described in Molluscs, I have not been able to determine, but hold it for probable.

Fig. 32 is a camera lucida drawing under $^1/_{18}$ in. Homogeneous Immersion. In the other figures in the plate the epidermis is represented somewhat diagrammatically as if it were composed of cells which are cylindrical along their whole length.

The nuclei of these epithelial cells are pretty large and rounded, and stain deeply. When a well preserved section of the epidermis is examined under very high power, such as that of an $^1/_{18}$ in. Hom. Immersion, the protoplasm of the cell is seen to be finely striated, the striae passing from the nucleus to the external surface (fig. 32). This striation is the optical expression of fine protoplasmic threads, which are indeed the cilia, or rather direct processes of them. Thus the cilia pass through part of the protoplasm of the cell, and are directly connected with the nucleus[3].

In fig. 31 which is part of a section of the skin certain curious rods are seen, these I take to be a sort of sense organ, probably of touch. The preparation is from an animal killed and stained with osmic acid. It is seen that these sense organs consist of short spindle-shaped rods of considerable length. They are composed of chitin, and show a double contour, and hence are hollow. They are set directly on the cuticula, not

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[1] l. c. [2] l. c.

[3] These fine striae are not well shown in the figure.

very widely apart. They are not very numerous, and in the whole series of sections of one animal not more than seven or eight were found. The only case in which I found them was in a perfectly normal individual *M. glabrum*, killed with osmic acid. I have never found them before or since. Their only possible function must be that of touch.

It is very curious that they should only have been found in one individual, and this fact I can only explain by the supposition that they are disappearing sense organs. In the particular individual in which they were found their presence may be due to a reversion to an ancestral condition. Their absence in other individuals cannot be explained as due to bad preparation, for they were not to be found in specimens prepared in exactly the same manner as this particular individual, and indeed prepared with special reference to these supposed sense organs.

Nervous System.

The nervous system was first discovered by Lovén, and was described more in detail by Semper[1] in *M. glabrum*. Semper referring to its finer structure says: »Es besteht nämlich aus einer feinkörnigen äußeren ziemlich dicken Schicht, und einer centralen länglichen Masse, welche innen ziemlich viel dunkler gefärbt ist, als die Rindenschicht und aus zelligen Elementen zusammengesetzt zu sein scheint. . . . An frischen, in Seewasser untersuchten Präparaten sieht man jedoch deutlich, dass diese centrale Masse ganz abgeschlossen ist und auf keine Weise durch Fasern mit den Nerven in Verbindung steht.« The central mass described by Semper was considered by Graff[2] to be made up of large ganglionic cells.

With regard to the finer structure of the nervous system, it is indeed divisible into a central dark mass and an outer lateral much lighter portion. The lateral mass however is not »feinkörnig«, but rather composed of numerous nerve fibres and connective tissue elements (figs. 33 and 34). It contains but few cells, and these apparently all or mostly connective tissue cells. As one might expect the central mass is not closed off from the lateral parts, but is a direct continuation of them. It is a dense cellular mass made up of connective tissue cells and nerve cells. In some cases it shows traces of a division into two lateral halves by means of connective tissue septa which pass part way into the central mass (fig. 33).

The connective tissue cells are numerous, rounded or slightly oval

[1] l. c. p. 54. [2] l. c. p. 56.

and thickly packed. The ganglion cells (*g.c*) are large, with large nucleus and deeply staining nucleolus. They are few in number, never more than six or eight being seen in one transverse section.

They possess an undetermined number of processes which end in nerve fibres. These ganglionic cells seem to be confined to the portion of the nervous system from which nerves, and especially large nerves are given off. We have indeed in their arrangement traces of a series of ganglia, which however by degeneration have lost their primitive character of segmental ganglia.

The whole nervous system is enclosed by a layer of connective tissue, and lies in the connective tissue under the alimentary canal (fig. 37 and 38).

With regard to the number of nerves, their course etc. described by Prof. GRAFF[1], I have nothing new to add, and can only say that I have failed entirely to find any oesophageal collar. If such a collar existed, and especially if it had the form and relative size figured by GRAFF in Plate XI fig. 8, it could hardly escape being seen in sections. Prof. GRAFF only found it once in *M. cirriferum*, and then under the dissecting microscope. In spite of all a priori probabilities and all possibilities of its presence I cannot but think that at present the evidence is a little uncertain.

Against a priori reasoning in favour of its presence it may be urged that *Myzostoma* has no head and no head sense organs, hence can have no use for a supra-oesophageal ganglion and nerve collar or for either. The rest of the nervous system, which chiefly supplies muscles, in spite of its size, is not very highly developed. Indeed the whole condition of the nervous system points to degeneration.

Alimentary Canal.

A few words as to the character of the epithelium in different portion of the canal. The epithelium is cylindrical throughout, but on the dorsal side of the stomach it is not so high as and more square than on the ventral (fig. 35). This condition is reversed in the intestine, there it is the ventral portion which is flattened while the dorsal portion is composed of long narrow cells (figs. 37 and 38).

[1] l. c. p. 56.

Development.

The egg.

The ovary of *Myzostoma* is not a well defined organ. The ova are scattered and lie in and among the connective tissue. The development of the ovaries is not known, a gap in our knowledge which I hope later to fill up, but since the ovary fills up all the body space, not occupied by the testes and nervous system, between the alimentary canal and the skin, it can be regarded as derived from the epithelium of the body-cavity, which by the great development of the sexual organs has become greatly modified so that it has practically as a body-cavity disappeared, only the parts concerned in the sexual function remaining. Perhaps rather we may say the whole of the epithelium of the body-cavity has acquired the function of producing sexual cells.

In a transverse section of a mature hermaphrodite one meets ova in all stages of development lying in nests of connective tissue (Pl. 2 fig. 36). The youngest ova are small, possess only a dark staining nucleus, and no germinal spot, and are hardly distinguishable from connective tissue cells.

Soon a germinal spot is formed by the collection of the chromatic substance of the nucleus, and the growth of the achromatic substance. Thus even in young ova of 0,008 mm in diameter we find a darkly staining germinal spot (fig. 36) enclosed in a germinal vesicle of fairly large size. The germinal vesicle has a distinct membrane and clear non-staining contents. The protoplasm of the egg is somewhat granular. In the course of its development yolk is formed in the egg, perhaps in the way described by WILL[1] in Amphibia and Insects, for I have noticed and figured small bodies in the germinal vesicle and in the protoplasm of the egg (fig. 39 *k*, *f*, *p*) which seem to proceed from the germinal spot. These bodies appear to me to be exactly analogous to, and to have the same characters as those in Amphibia and Insects. My friend's complete paper is not yet published, so I will only draw attention to the fact. In the ripe egg (fig. 1) one sees usually a dark-coloured mass in the protoplasm, which I identify as the so-called yolk-nucleus of other animals. It is situated at the vegetative pole of the egg, and has usually not very well defined outlines; but in some cases of hardened and stained eggs it seems to have a curved sharp

[1] WILL, Über die Entstehung des Dotters und der Epithelzellen bei den Amphibien und Insecten. Zool. Anzeiger. 1884. No. 167. 168.

well defined form. Probably this is due to the effects of reagents. The mature eggs, when squeezed out of the body in mass, are of a delicate pinkish colour. In diameter they are in the average 0,036 mm with germinal vesicle of 0,012 mm and germinal spot of 0,004 mm diameter.

Spermatozoa.

Under this head I will only say that one very often notices quantities of undeveloped mother-cells of Spermatozoa in the vasa deferentia of the male of *M. glabrum*.

Fertilisation.

The usual preliminary to fertilisation here as in other cases is the formation of the polar bodies. Usually there are two in number. About a quarter, more usually half an hour, after the egg leaves the body the first polar body is pinched off (fig. 2). The egg becomes somewhat flattened at one pole, and a small perfectly clear vesicle is pushed out. Shortly after the formation of the first the second polar body is also formed, and the egg is ready for fertilisation (fig. 3). The second polar body is often larger than the first. Among my notes is one to the effect that the polar bodies appear sometimes to be formed after segmentation has actually commenced. If this be the case it would lend some support to the view, advanced I think by one of the Professors Hertwig, that the formation of the polar bodies is to be regarded as abortive attempts at segmentation. After fertilisation the egg becomes surrounded by a membrane.

Segmentation.

Segmentation usually commences three hours after the eggs are laid. It is complete but unequal, and indeed follows the usual Chaetopod type. It has already been fairly described some 18 years ago by Metschnikoff[1], but as there are some additions to be made, and in order to give a complete picture of the whole course of development, any recapitulation may not be out of place. Segmentation usually begins in the artificially fertilised egg two or three hours after it leaves the body. The fertilised egg lengthens somewhat, the usual nucleus spindle is formed, and division takes place. Two segments are formed, one of which, viz. that at the animal pole of the egg is very much smaller than the other, being in fact not more than a quarter the size of the other. The yolk and yolk-nucleus are confined to the larger seg-

[1] l. c. p. 237.

ment (fig. 4). A period of repose then ensues. Fifteen minutes after the first division, the larger of the two segments divides and once more in such a manner that one of the resulting segments greatly exceeds the other in size (fig. 5). Thus there are now three segments all of unequal size, viz. a small segment as the result of the first division, a larger segment and one double the size of this, the latter two formed in the second division. Again there is a pause about a quarter of an hour and then the rhythmic act of segmentation proceeds. In the next division the smaller of the two last formed segments is alone concerned. It divides into two pretty equal halves. At this stage (fig. 6) the segmenting egg consists of three pretty equal small spheres; the future epiblast, and one large hypoblastic sphere, the latter containing the yolk, and also the yolk-nucleus, which at this stage is still visible.

The succeeding stages vary somewhat, tho' the final result is the same. Indeed here we have variations similar to those recorded by Wilson[1] for *Renilla*. The variations here are not so numerous, indeed they are only two in number. The first mode is a successive division of the epiblastic spheres commencing with the one first formed, that is, with the smaller of the two first formed segments. Its division is followed by that of the other two epiblastic spheres, one after the other (figs. 7, 8, 9).

In the second mode the whole three of these epiblastic segments may divide simultaneously (fig. 9). In both cases we get as the result one large hypoblastic segment, and six small epiblastic segments, which form a hood or cap over the former (fig. 9). The hypoblastic segment now divides into two equal spheres (fig. 10), in some few cases this division only takes place after some of the epiblast spheres have again divided (fig. 11). The epiblastic spheres now all divide and in doing so grow more and more over the hypoblastic cells. The division goes rapidly on, but is very difficult to follow in such small elements. It results in the enclosure of the hypoblast cells within a layer of epiblast cells. The point where the epiblast cells meet, viz. the blastopore, closes, but on its site is formed the future mouth. A stage just before the closure of the blastopore is shown in optical section drawn under $^1/_{18}$ in. Leitz Homogeneous Immersion in fig. 13. Here the layer of epiblast cells encloses four hypoblast cells, and two mesoblast cells, the latter being darkly coloured for the sake of distinction. All these six cells have been formed by the division of the two hypoblast cells.

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[1] E. B. Wilson, Variation in the yolk-cleavage of *Renilla*. Zool. Anz. 1882. p. 545—548.

Segmentation is completed some few hours after fertilisation, but the embryo is still enclosed in the vitelline membrane. Soon the epiblastic cells acquire cilia and the embryo rotates within the membrane (fig. 12). About twenty-four hours after the egg is laid the embryo is hatched and the free-swimming larval stages are entered upon.

Larval History.

The larval history may be divided into three well marked periods. Firstly the period during which the larval ciliation is not split up into rings. This period extends over the second day after the egg is laid. — Secondly, the period in which rings of cilia are differentiated, and in which the larva is still free-swimming. This period extends from the end of the second to about the eighth day or thereabouts. Lastly, the period in which the larva is no longer free-swimming but has its seat on a *Comatula*.

Earlier larval Stages. — First period.

When the embryo leaves the egg to enter upon its free larval existence it is a minute, somewhat oval, ciliated semitransparent being of about 0,05 mm in length (fig. 14). Its body is made up of an epiblast of one layer of ciliated cells, and of certain larger and darker cells, few in number, enclosed by the epiblast cells. These larger cells are the future hypoblast and mesoblast (fig. 15). Alimentary canal and mouth are not yet developed, and the blastopore has closed. A cuticle is present, of a structureless nature, through which the cilia pass.

The ciliation even at this early stage is not simple and uniform. The larva figured by METSCHNIKOFF is in this respect not correct. The ciliation is difficult to make out, but appears to have much the same sort of peculiarity of arrangement as in the adult. The cilia are not uniformly scattered over all the cells of the epiblast, but are arranged in bunches or clusters, and are somewhat stiff (fig. 14). Nor is it arranged over the whole body, for the future anal region is destitute of cilia (figs. 14 and 15). The larva soon lengthens, and assumes somewhat of a pear shape (fig. 16). Towards the end of the second day, or early in the third, the mouth is developed as an epiblastic invagination on the site of the blastopore. This invagination grows inwards to meet the stomach which has meanwhile been formed as the result of division of the hypoblast cells. The mesoblast cells have also probably increased in numbers, and a little later furnish muscle-cells to the stomodaeum and stomach, some portions of the primitive mesoblast however still remain

in an embryonic condition, and these, as will be seen, later lie on each side of the alimentary canal in the hinder region of the larva. The anus too, is now formed at the narrow or pearshaped end. To the ventral side of the anus a papilla grows out, and on the dorsal side of this the anus opens during larval life.

Middle period of Larval history.

The larva now enters upon a series of changes by which it is specially fitted for a course of free larval existence. These changes consist chiefly in the development of provisional setae, and in the restriction of the ciliation to certain regions of the body. These things occur soon after the formation of the mouth. The cilia are absorbed except in certain definite regions. On the »Scheitelfeld« or apex of the praeoral lobe of the larva the cilia become diminished in numbers, but at the same time they grow very much in length, and then form a crown of stiff cilia on the Scheitelfeld (figs. 18, 19, 20). They are few in number, long and fine and radiate somewhat from the centre, adding much to the beauty of the larva.

I have never been able to distinguish a ring of praeoral cilia, and in the absence of this I fear that the *Myzostoma* larva varies from HATSCHEK's[1] typical Annelidan larva. But seeing that in but few Annelidan larvae this complete series of rings of cilia is developed, the absence of this particular ring cannot be taken as strongly militating against the placing of *Myzostoma* among the Chaetopoda. No praeoral circlet of cilia exists in this or any subsequent stage unless we regard the crown of cilia in the praeoral lobe as the remains of one. This we are hardly justified in doing, as will be pointed out later. The region in front of the mouth, that is to say the praeoral lobe, in the larva is very small and not well developed. Indeed the absence of any well marked head region on the adult is reflected in part in the larva. But a very well developed post-oral ring of cilia occurs (figs. 20, 21). The cilia are long, mobile and pretty thickly set. They are especially numerous and long directly behind the mouth on the ventral side.

Further back we get a praeanal circlet of long cilia directly in front of the anus, and a number of long stiffish cilia on the post-anal papilla (figs. 21, 22).

Simultaneously with the above alteration in the ciliation the larva

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[1] HATSCHEK, Studien über die Entwicklungsgeschichte der Anneliden. Arbeiten a. d. Zool. Institut zu Wien. Bd. I. Heft III.

acquires provisional setae. These begin to arise towards the end of the second day (fig. 17). They probably arise in epiblastic sacs. On each side of the body and at some distance behind the mouth a pair of chitinous rods are developed. The two setae on each side are formed close together and at the same time. They grow rapidly and when the larva is three days old they are already of fairly considerable size (figs. 19, 20). But they have not then attained their full growth, but continue to grow until the larva is about seven days old (figs. 21, 22). At this time they are very long, even longer than the larva itself.

Subsequent to the third day the setae are usually increased in number, but there is never in the larva a segmentally arranged series of setae, such as GÖTTE[1] described and figured for *Nereis Dumerilii*. A rough sketch of GÖTTE's fig. 19, Plate VI I have given on fig. 29. With the formation of the provisional setae the development of muscles to move them becomes necessary. These latter appear to be formed by the proliferation of part of the primary mesoblast. So that on each side of the body muscle-cells are given off from the mesoblast, and these become attached to and lie in close connection with the inner wall of the setiferous sacs (figs. 27, 28).

At this stage the thickening of the epiblast of the frontal lobe also begins. In other words the larval nervous system begins to be formed. When these things have taken place we have a larva such as is represented in figs. 19, 20 and 21. Fig. 19 represents a larva of *M. glabrum* of 4 days and fig. 20 one of *M. cirriferum* in the same stage of development. The two figures are given so as to admit of the comparison of the larvae of both species. A comparison which readily leads to the conclusion that at this stage the development is practically the same in both species.

The larva of three days is in a condition to provide for its own nutrition, and so is pretty well fitted up for a free existence. It possesses fully formed mouth, alimentary canal and anus. It has two rings of cilia, one immediatety behind the mouth to provide its nutrition, and one in front of the anus to facilitate its locomotion. In addition it has other locomotive organs in the provisional setae, which are well provided with muscles, and subserve the double purpose of locomotion and protection.

Further the larval nervous system is pretty well developed, and

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[1] GÖTTE, Abhandlungen zur Entwicklungsgeschichte der Thiere. 1. Heft. Taf. VI Fig. 19, 20.

on the surface of the praeoral lobe are planted a number of long fine, stiff cilia which are probably processes of the larval nervous cells, and hence may be regarded as larval sense organs. All these things are figured in figs. 19, 20, 21, 22. During the following days, from the third to the seventh the development consists merely in an increase in size of the larva and in the further differentiation of the organs already present.

It might a priori be expected that on the third day or subsequently traces of segmental organs would be formed. This is however not the case. In spite of very much time and trouble spent in attempts to find such organs the result at all stages of the larval history has been purely negative. I can only conclude that in *Myzostoma* segmental organs are not formed during the larval development. This absence of head kidneys cannot I think be considered as reason for shutting *Myzostoma* out of the group of Chaetopoda, for judging by the observations of GÖTTE it shares this negative character with *Nereis Dumerilii*, at least in his work segmental organs are neither mentioned in the text nor figured in the plates. Further at the time of writing this so little is published concerning the occurrence of larval segmental organs among the Chaetopoda that failure to find them in the larva of *Myzostoma* need occasion little concern. In figs. 21, 22, 23 and 24 larvae from the fourth to the seventh day after fertilisation are figured. The main difference they show from three days larvae consists in increase in size.

The larva can now move about in search of food. Its nervous system has reached a fair development, and is well marked in every individual (figs. 23, 24, *n.s.l*). In fig. 24 especially it is a prominent feature. This figure and fig. 23 show too a ventral thickening of the epiblast, which has now formed. This is the foundation of the future ventral ganglionic mass. The sense hairs on the praeoral lobe have not grown and remain in much the same condition as on the third day (figs. 21, 22, 23, 24, *s.h*).

In fig. 24 is also seen a muscle cord, which like that described by HATSCHEK[1] in *Polygordius* passes from the apex of the praeoral lobe to the head end of the larva.

The alimentary canal is now very fully developed, and has acquired the foundation of the future proboscis. This latter is at this stage not protrusible but is very muscular. It has been formed by the develop-

[1] HATSCHEK, Studien über Entwickl. der Anneliden. Arbeiten a. d. Zool. Institut zu Wien. Bd. I. Heft III. p. 31.

ment and arrangement of muscle cells around the stomodaeum. The stomach (fig. 21, 24) is large and well marked off from the stomodaeum and short intestine.

In some larvae the primitive two pairs of setae are the only ones developed, and exist still at the fifth or sixth day, having only increased in length. In most cases however additional setae are formed, and the larva of five days very often has free pairs of long setae, which usually equal the length of the larva itself and very often exceed it (fig. 21, 22). The anal papilla is now well developed and retractile. The anus still opens on the dorsal side of it (figs. 22 and 23). Two sections of five days larvae are given in figs. 27 and 28. In them it is easy to recognise the larval nervous thickening of the praeoral lobe and the muscles and sacs of the setae (*se.s*). But they also show another point. This is that certain of the mesoblast cells remain in an embryonic state as two bands, and are not functional in the larva. These cells (*me.r*) first take on a renewed activity on the later stages. and form in part or entirely the musculature of the permanent feet. We shall have occasion to refer to these later on.

In aquaria placed in the working room of the zoological station of Naples the period of free larval life appears to last for seven or eight days. This is of course at the relatively high temperature, compared with that of the sea, obtaining there. Whether it be of longer duration in the natural state at the sea bottom is not determinable. The larvae appear to be exclusively bottom forms. They swim and creep about the bottom in search of food. This fact coupled with their minute size, never more than 0,08 mm in length, accounts for their not having been previously observed. Small as they are they could hardly have escaped observation had they been surface forms. They are somewhat sluggish creatures and do not move about very much. When they do move it appears to be sometimes by the aid of their setae, sometimes by the aid of their cilia.

Third period of larval history.

The larva described in the preceding pages attains its full development as a larval form when about four days old. When about seven days old its characters begin to alter. Already in fig. 24 the setae are partially cast off.

It is now preparing to take up its adult habitus on a *Comatula*. To this end the provisional setae are cast aside (fig. 23) and the larva moves about with a worm-like motion, reminding one very much, if the

comparison may be made without danger of falling into morphological errors, of the crawling of a Tardigrade.

The rings of cilia become again broken up. Fig. 25 shows a larva of eight days. It has lost its setae but has not developed any permanent limbs. However it appears to possess two somewhat ventrally placed processes (*p.p*) which may aid it in its endeavours to attach itself to a *Comatula*. It is the only larva with these processes which I have observed, for usually I was unable to keep them living for so long as in this particular case. Hence the possibility of its being a pathological larva must be borne in mind, and for myself I do not believe it is a normal stage.

In no case have I found larvae in a free state with permanent legs developed or even with traces of them. On the other hand I have found on a *Comatula* a larva (fig. 26) in which only the rudiments of one pair of limbs are present, and these of so small a size that it is inconceivable that they could be of any use to it in finding its way to a *Comatula*, or in retaining its place when there. Hence it may be concluded that in the free state no further stages of development are passed through, and that the rest of the development takes place on the *Comatula*. This conclusion I think may be accepted in spite of the fact that I have been unable to trace actually the passage from the free state to that on the Crinoid. The difficulties which prevent success in all attempts in this direction are twofold: the extreme smallness of the larvae and the well known difficulty of keeping chaetopod larvae living for many days together. In any case the stages not observed cannot be of any great importance, since it is pretty certain that no permanent claws are developed until the larva is on its host. And certainly no other organs are developed till then.

And now it becomes a very interesting question as to how the larvae get on a *Comatula*, or even find one at all. It is certain that when in possession of provisional setae and ciliated rings it does not take possession of its host, for if it did, such larvae would be found among the animals which fall off in the alcohol when a *Comatula* is killed in the way described in the earlier pages of this paper. But no larvae with provisional setae are found there, and the youngest found (fig. 26) has traces of one pair of permanent legs.

The muscular processes figured in the one larva (fig. 25) even if they be such, can hardly be of much service. And indeed I am inclined to think that the larva finds its host in a much simpler manner than by any use of its own limited senses or of its own muscles. Probably the

larva finds its way to its host purely by chance. That is to say it is merely carried to the *Comatula* by means of the currents of water caused by the arms of the latter. If a larva, and especially such a minute one as that of *Myzostoma* where caught by this current it would in the natural course of events be carried along the ambulacral groove towards the mouth. If it were able by means of claws, or of some secretion, or even by the use of its cilia, to save itself from being devoured, it would stand a fair chance of further development, and would have the means of increasing rapidly its size in the food current passing along to the mouth of its host.

How it is able without claws to hold its own against the forces tending to draw it into the mouth of the *Comatula* is not easily answered. But that it does so in some way is certain. When possessed of two pairs of claws, its position is pretty secure, for I have observed that at this stage they have a very firm hold on *Comatula*. In the tanks of the aquarium of the Naples zoological station, the *Comatulae* sit in great numbers on the stems of dead corals. But in addition a considerable number take up their position near to or on the floor of the tank. Now it has been shown that the larvae of *Myzostoma* frequent the bottom, and thus *Comatulae* on or near the bottom will be in a better position for becoming host to larvae of *Myzostoma* than those further away. Some observations made in the aquaria seem to show that this is really the case, and thus that the current theory has some foundation. At one time for some days on account of the stormy state of the sea, freshly caught *Comatulae* were not to be had, and so I was obliged to fall back upon those contained in the aquarium of the station. It was then noticed that those *Comatulae* which were sitting on or near the bottom were much more invested with *Myzostoma* than those which clung to the sides of the tank or to the stems of the corals. It has been shown in the preceding pages that the larvae are bottom forms, and a priori it is what one might expect that individual *Comatulae* which frequented the bottom would be much more invested than those living at some distance from it. In this connection it may be mentioned that a *Comatula* seldom or never changes its position if not disturbed. I have observed a *Comatula* sit exactly in the same place on the stem of a dead coral for over a month without changing its position. If this current theory be true an interesting result would follow, viz. that only such larvae as were not too large to be carried by this current would obtain a host and so be in a position for further development. Thus the size of the larvae would be kept within certain limits. Perhaps this is the reason, why the larvae are so small.

Chance is an element, which enters into the life history of other parasites besides *Myzostoma*. One need hardly mention the eggs of tapeworms etc.

With its acquisition of a host the larva is led to further development, the end of which is the attainment of the adult form. The cuticula which is not so well developed in the earlier larval stages attains now to some thickness (fig. 45). The ciliation is of the same character as that of the adult. It is no longer confined to definite regions of the body but as in the adult consists of cilia arranged over the whole body in branches or groups.

Certainly the most striking changes consist in the development of the legs. They are formed in the hind region of the larva. This region without taking on at first external segmental characters begins to form segmental appendages. The legs are formed from before backwards, in what are probably epiblastic sacs. At first the setae are straight and without hooks, but they soon become hooked, the direction of the hook being inwards towards the median line. The anterior pair are first formed, and then the other four pairs in succession from before backwards. In addition to the external phenomena observed in the formation of the limbs, there are certain internal processes going on which concern the mesoblast. It was pointed out when discussing the larva of five days old that certain cells of the mesoblast remain in an embryonic state, apparently without function in the larva (figs. 27, 28).

These cells, which occupy a position on each side of the alimentary canal in the hinder part of the larva, now become active, divide rapidly and form a mass of cells, which are well seen in figs. 41, 44 and 48. With the formation of the first pair of legs a certain portion of this mass on each side becomes segmented off from the rest to form the future musculature of the legs (fig. 48). So too in the case of each additional pair of legs. Thus the mesoblast becomes segmented. A little later this internal segmentation extends in part to the external portion of the body, at least in *M. cirriferum* (fig. 48). But in later development the external segmentation is not obvious and in this absence of external segmentation *Myzostoma* resembles *Polygordius*.

During the whole period of the development of the legs the alimentary canal is quite simple in character, and the stomach has no diverticula. The proboscis increases in size and becomes more retractile than in the earlier stages. It is only sometime after the complete complement of legs is formed that the alimentary canal acquires its diverticula.

Nervous System.

The nervous system apparently consists in the later development of a ventrally placed mass of cells, which during all the stages of development of legs is closely connected with the skin. In spite of much search I have been unable to find traces in the later stages of the functional larval nervous system, and believe it entirely disappears. Indeed my researches on both larva and adult lead me to the conclusion that no supra-oesophageal ganglion is present in the adult, nor have I been fortunate enough to find any trace of the oesophageal ring described by Graff[1]. So far as I can judge the nervous system of *Myzostoma* is as follows. In the larva it consists of a median thickening of the epiblast of the apex of the praeoral lobe. In the later stages of larval life this larval nervous system completely disappears. In the adult the nervous system consists solely of a ventral mass of cells and connective tissue, which mass as will be shown later presents traces of an origin from the fusion of several ganglia.

Bergh[2] has shown that the »Scheitelplatte von *Nephelis* ist demgemäß ein vergängliches Embryonalorgan, dessen Zellen sich überhaupt nicht als Ganglienzellen ausbilden, und das Gehirn entsteht (wie schon Semper angegeben) aus den von Anfang an paarig sich entwickelnden und erst später über dem Schlunde sich vereinigenden Kopfkeimen.«

My own researches on *Myzostoma* lead me to accept the above view. Though the »Scheitelplatte« of *Myzostoma* is functional as brain in the larva, I believe it has nothing to do with the formation of the adult nervous system. The larval nervous system like the »Scheitelplatte« of *Nephelis* is only a transitory embryonic organ. In the adult no supra-oesophageal ganglion is developed and no rudiments of it are laid down in the larva. In fact one is led to the conclusion that the supra-oesophageal ganglion of *Myzostoma* in consequence of retrograde development and degeneration has completely vanished from the individual ontogeny.

On the development of *M. cirriferum*.

In the preceding pages the development of *M. glabrum* has been chiefly considered, and now this must be compared briefly with that of

[1] l. c. p. 56.

[2] R. S. Bergh, Thatsachen aus der Entwicklungsgeschichte der Blutegel. Zool. Anz. 1884. Nr. 164. p. 93.

M. cirriferum. METSCHNIKOFF's paper[1] on the development of the group referred chiefly to *M. cirriferum*. I have not given in detail the development of this species, firstly because the segmentation has already been described and figured by METSCHNIKOFF, and secondly, because the development differs only in the minutest details from that of *M. glabrum*. A few words may be added here. The egg does not differ appreciably in size from that of *M. glabrum*. The eggs of *M. cirriferum* however seemed to be a little more transparent than those of *M. glabrum*. The segmentation is practically identical in both species. But when the first two segments are formed the larger of the two does not exceed the smaller in size to the same degree as in *M. glabrum*. This is even more the case when three segments are present, then all three do not differ much in size. Still the future hypoblast cell is larger than the other two. This has been correctly figured by METSCHNIKOFF. It is due perhaps to the fact, that the egg of *M. cirriferum* possesses rather less yolk than that of *M. glabrum*. Further it may be remarked that in METSCHNIKOFF's fig. 6, pl. XIII one of the segments has obviously been overlooked and is not figured. My figure 10 shows this stage.

In the further development the larvae are exactly alike in both species. In fig. 20 I have given a larva of *M. cirriferum* at the age of three days, and by its side fig. 19 one of *M. glabrum* aged four days. The resemblances, almost amounting to identity, will be obvious at once. It is the same in the further development.

Systematic position.

It may be questioned whether any animal has been so pushed about from one division of the animal kingdom to another as *Myzostoma*. The most diverse views have been and are still held as to its proper systematic position.

This is no doubt due in great part to the absence of any complete knowledge of its development. But now that this gap is in great part at any rate filled up, it may be hoped that the genus will be allowed to enjoy a little well-earned repose.

Its discoverer, F. S. LEUCKART, regarded it as a Trematode. JOHANNES MÜLLER and LOVÉN were inclined to place it among the *Tardigrada*, LOVÉN at the same time holding it to have affinities with the higher Annelida. SIEBOLD looked upon it as a link between the *Chae-*

[1] l. c.

topoda and *Trematoda*, but placed it among the *Chaetopoda*. By Van der Hoeven it was classed among the parasitic *Crustacea*, while Diesing classed it with *Histriobdella* among the Leeches. It has been placed among the *Turbellaria* by M. Schultze, among the *Crustacea* by Leydig and Carus, while Semper considered it impossible without knowledge of its development to determine its position with any pretension to certainty. Nevertheless his figure of a larva with two pairs of legs, and some external resemblance to a *Nauplius* led Carus and others to the conclusion, that the group had some relationship with the *Crustacea* — a view held so recently as 1881 by Prof. Hensen in Hermann's Handbuch der Physiologie. Bd. VI. p. 99, who speaks of it as a small »Krebschen«. Four Zoologists have in their works recognised its true nature. R. Leuckart, Metschnikoff, Claus and Bütschli all agree in placing it among the *Chaetopoda* — a position which its developmental history most certainly entitles it to. Graff in his Monograph of the Genus places it near the *Tardigrada* and unites the *Tardigrada*, *Linguatulidae*, and *Myzostomidae* in one division as *Stechelopoda*.

This view is repeated as the result of his latest researches on the Challenger- and other *Myzostomidae* in the Tageblatt der Versammlung der deutschen Naturforscher und Ärzte in Freiburg 1883, report of First Meeting.

It would be useless to enter into a long discussion of the reasons for refusing to place *Myzostoma* among the *Trematoda*, Leeches, *Turbellaria* or *Crustacea*. They are obvious on the face of it, for the development as described in the preceding pages and figured in the Plates cannot be made to fit in with the development of any of these groups. And thus there only remain to discuss the claims of the *Tardigrada* and *Chaetopoda*. Reasons must be given against their relationship to the *Tardigrada*, because they have been placed near these by the greatest authority on the genus, Prof. Graff. So far as I know the only paper we possess on the development of the *Tardigrada* is one published in 1851 by Kaufmann[1]. The development is there described and figured as being a direct one, and in no way does any part of the segmentation and complicated development of *Myzostoma* allow of comparison with that of *Macrobiotus*. Nor are the superficial resemblances in adult anatomy such as really to justify an assumption of relationship. Some species of *Myzostomidae* like the *Tardigrada* are hermaphrodite, but

[1] Zeitschr. f. wiss. Zool. Bd. III. — A remarkably good paper considering that it was written long before our modern methods of research were invented.

some such as *M. cysticolum* etc. are bisexual. Neither are the sexual organs built on the same plan in both groups. In the *Tardigrada* the ovary is a small well defined compact organ producing a few large eggs, according to KAUFMANN seven or eight in number. In *Myzostoma* it is not a compact organ, but is scattered throughout the body and produces great numbers of minute eggs. The complicated male organs of the *Tardigrada* to an even less degree show resemblances to those of *Myzostoma*. In the latter the legs are not built on the same plan and are not equal in number to those of *Tardigrada*. The *Myzostomidae* are ciliated, the *Tardigrada* not.

But if all anatomical likenesses were granted there would still remain the insurmountable obstacle of the development. The larva of *Myzostoma* with provisional setae is undoubtedly allied to the Chaetopods. Indeed the only group to which it can belong is the *Chaetopoda*. If we compare it with GÖTTE's larva of *Nereis Dumerilii*, a rough copy of which is given in fig. 29, the resemblances will be obvious enough. Both have a praeanal ring of cilia. *Nereis Dumerilii* has also a praeoral ring, while *Myzostoma* has a postoral. Both have mouth, simple alimentary canal and anus. Both have a thickening of the epiblast of the praeoral lobe which functions as the larval nervous system. Both have also a similar ventral thickening of the epiblast, which is the rudiment of the future ventral ganglia.

Both have provisional setae, the only difference here being that in *Nereis Dumerilii* the larva is segmented, while in *Myzostoma* it only becomes so in the later development. So in *Myzostoma* the larval setae are not arranged as in *Nereis Dumerilii*. The latter possesses an eye, while *Myzostoma* does not, but then in *Myzostoma* the region in front of the mouth is somewhat rudimentary and in this rudimentary condition of the praeoral lobe one sees the reason of the main difference between *Myzostoma* and more typical Chaetopod larvae. Owing to this too the praeoral ring has disappeared.

In neither *N. Dumerilii* nor *Myzostoma* are segmental organs to be found, and this negative character obtained in both *Myzostoma* and a true Chaetopod, can furnish no grounds for refusing to classify *Myzostoma* with the Chaetopods.

As to other resemblances in both *N. Dumerilii* and *Myzostoma* the segmentation is complete but unequal, in both it results in an epibolic gastrula, and probably in both the mesoblast arises in the same way. Most, indeed, if not all of the characters of *Myzostoma* speak for its union with the *Chaetopoda*. Its development is quite that of a Chaeto-

pod. As in them the segmentation is complete but unequal, a gastrula arises by epibole, the mouth probably arises on the site of the blastopore, a ciliated larva, which later acquires special bands of cilia and provisional setae, leaves the egg. The functional larval nervous system arises as a thickening of the praeoral lobe. In the adult the skin is that of a Chaetopod and the permanent limbs are easily derivable from Chaetopod setae. The alimentary canal is such as one often meets with among *Chaetopoda*.

The nervous system is reducible to a series of fused ventral ganglia. Supra-oesophageal ganglion, and possibly also the nerve collar have disappeared in consequence of loss of sense organs etc. due to parasitic habits. As a consequence too, of parasitism, the sexual organs have undergone great changes, and along with that the segmental organs have partly disappeared.

The ovaries are best regarded as arising from the epithelial lining of the body cavity[1], which they have by hypertrophy completely obliterated. The oviduct opening into a cloaca may perhaps originally have been formed from two segmental organs, for the cloaca is an epidermic invagination, and if it were obliterated the oviduct would open on the median line. The two male ducts are much more easily referable both from position and structure to segmental organs, which still open into the modified remains of the body cavity. In fine I agree with the great Russian naturalist METSCHNIKOFF, who says[2]: »Ich betrachte dieses Thier (*Myzostoma*) als Repräsentanten einer besonderen Chaetopoden-Gruppe, die *Chaetopoda ectoparasitica* heißen können.«

It is indeed perhaps impossible to place the genus near any particular family of Chaetopods. In its development it has resemblances to that of *Nereis*, and perhaps may be classed as a special family of the *Errantia*. And so adopting CLAUS' classification[3], we create a family of *Myzostomidae*, which at present only includes the genus *Myzostoma* with its numerous, about 30, species. The characters of the family being the following: Parasitic Annelids, mostly hermaphrodite, but some few species unisexual. Body flattened and disc-like with short cirri on the margins. Five pairs of legs, converted into hook-like organs. Proboscis and branched alimentary canal. Segmental organs only represented in the ducts of the reproductive organs. Development indirect with larval metamorphosis.

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[1] I hope soon to settle this and some other points more definitely.

[2] l. c. p. 243. [3] l. c. p. 498.

Notes on the Biology of the Genus.

If *Comatulae* be taken from various parts of the bay of Naples the number of both species of *Myzostoma* found on them will be found to vary with the place of capture. In the impure water near the shore the *Comatulae* are infested with very few *Myzostomidae*, while the opposite extreme is reached in those caught in the clear pure water near the island of Nisita, where most of the *Comatulae* are infested with *M. cirriferum* and many of them also with *M. glabrum*. Indeed *M. glabrum* is pretty abundant in this spot, and large specimens are found. The numbers of the two species found on a given *Comatula* vary very much, but the statistics given under this head by Prof. GRAFF[1] — so far as they concern *M. cirriferum* — are not correct. *M. glabrum* is much more rare than *M. cirriferum*, and probably the relative frequency of its occurrence given by GRAFF is correct — that is that about every third *Comatula* is host to a *M. glabrum*. If a living *Comatula* be placed in alcohol a great number of *M. cirriferum* will fall of it, especially if the animal be shaken in it. Probably the usual number of *Myzostoma cirriferum* on one *Comatula* is on the average at least double the number ten given by Prof. GRAFF. In some cases great numbers may be found on one *Comatula*. In one example I counted on a disc and a small portion of the arms of a *Comatula* killed in sublimate not fewer than 23 large *M. cirriferum*. The remainder of the arms had been cut away, and probably those portions had many *M. cirriferum* on them.

The number of large *M. glabrum* crowded around and partly within the mouth of a *Comatula* is often such, that it is hardly possible that the host can get much to eat for itself. The food of *Myzostoma* is naturally limited to some portion of that of *Comatula*. It chiefly consists of Infusorians, Algae, Diatomaceae and other minute organisms. In fig. 35 is figured part of a transverse section of a male of *M. glabrum*, which has devoured and partly digested some of the eggs of the hermaphrodite on which it sat.

The time of reproduction does not appear to me to be confined to any particular season of the year. Although I have not investigated living *Myzostomidae* in summer and autumn it appears to me that GRAFF's view that summer is the chief period of reproduction, at any rate in Naples, is not correct. *Myzostoma* like many other parasites seems to be compelled to be continually in a state of sexual maturity

[1] l. c. p. 76.

during the whole year in order to preserve the continued existence of the species.

During the winter and spring I have examined great numbers of both species, and in all cases in which the animal was of fair size it was sexually mature. If GRAFF's view were correct, we should expect to find numerous immature individuals in the winter and spring and few mature ones, whereas great numbers of mature individuals occur. I have found naturally fertilised eggs in no small quantities in the middle of winter. In winter and spring one also finds young in great numbers. With regard to his assertion that at Trieste he has oftenest observed in autumn the sitting of a young one on the back of an old one, I can here only remark, that Prof. GRAFF's so-called young ones are no young ones at all, but fully developed males: the matter is dealt with fully in the next section.

The males of *M. glabrum*.

»It must have struck most naturalists as a strange anomaly that, both with animals and plants, some species of the same family and even of the same genus, though agreeing closely with each other in their whole organisation are hermaphrodite and some unisexual.« — DARWIN, Origin of Species. Sixth edition. 1880. p. 79.

SEMPER, in his paper on the genus *Myzostoma* [1], described how he once saw »ein kleines *M. cirriferum*, welches nur ausgebildete Zoospermien enthielt, in der Weise auf einem großen, mit entwickelten Eiern versehenen Individuum derselben Art sitzen, dass die eine männliche Geschlechtsöffnung ungefähr in die Nähe des Afters zu liegen kam«, and adds »spätere Untersuchungen müssen diesen Punkt aufklären«. The same phenomenon had previously been seen by O. SCHMIDT, and curiously enough set down by him as a character of *M. glabrum* that it possessed a knob-like process (Knopf) on the anterior end of the back.

SEMPER only observed it once and then in *M. cirriferum*. I have never observed it in that species in spite of much search, nor does Prof. GRAFF appear to have done so either. I have observed the phenomenon in *M. glabrum*, and must say against SEMPER's view that this so-called young one never takes up such a position that its male

[1] l. c.

genital aperture of either side comes to lie anywhere near the cloacal aperture of the animal on which it sits.

Graff [1] recognised Schmidt's »Knopf« »als ein auf dem Rücken des alten sitzendes Individuum derselben Art«. He further says: »Ich habe an meinen Spiritusexemplaren nicht selten, sehr häufig aber an lebenden Myzostomen in Triest diese Erscheinung wahrgenommen, welche mit dem Herbst an Häufigkeit zuzunehmen scheint, da ich sie nie so oft wie im September beobachtet habe, in welchem Monate in Triest nahezu ein Dritttheil der ausgewachsenen Individuen von *M. glabrum* mindestens je ein Junges auf dem Rücken trug. Doch fanden sich deren auch bis drei Stück auf einem alten. Dabei ist die Verbindung eine so feste und der Rand der Jungen so dicht dem Rücken der Alten angepresst, dass die Lostrennung der ersteren nicht leicht vor sich geht und jedenfalls nicht, ohne die (wie ich mich an Durchschnitten überzeugte) oft bis unter den Hautmuskelschlauch eingestoßenen Haken abzubrechen. Ich fand unter den aufsitzenden Individuen solche von mikroskopischer Kleinheit bis zu solchen von $1^1/_2$ mm Länge. Fig. 11 der Tafel I stellt zwei so verbundene Individuen dar, und man sieht, wie das Junge seinen Rüssel möglichst weit vorstreckt, um über den Vorderrand des Alten hinweg dem Mundrande der *Comatula* — der Vereinigungsort der Nahrungszuströme — nahe zu kommen. Die beträchtliche Größe, welche die so aufsitzenden Thiere erreichen, beweist am besten, dass zu dem Gedeihen des Parasiten eine directe Berührung seines Wirthes gar nicht nothwendig ist — er will in der That die Nahrungszufuhren mit ihm theilen. Findet nun das Junge, wenn es, seine freie Lebensweise aufhebend, sich zur Ansiedlung anschickt, den ganzen Mundrand der *Comatula*, an die es eben geräth, bereits besetzt, oder kommt es zufällig an einen Platz, wo bereits ein altes Thier sich festgesetzt hat, so krallt es sich eben ohne Schaden für seine Ernährung auf dem Vorderrücken dieses fest. Eine andere Bedeutung kann ich dieser Erscheinung nicht zuschreiben«[2].

I have quoted Graff's views on the matter at full length, because I am led to disagree with him in toto as to the nature of these so-called young ones. They do occur, but they are not young ones but fully developed males, usually with numerous fully developed and functional spermatozoa. In fact *M. glabrum* is not as all previous observers, including the latest Prof. Graff. have considered a simple hermaphrodite.

[1] l. c. p. 75. [2] l. c. p. 75—76.

but is hermaphrodite with fully developed and highly organised males (fig. 30).

In size these males vary very much from $^1/_{10}$ mm to about 1 mm in length, which is about the maximum. I have never found them larger than 1 mm, and two which I kept living on their host for over a month died without increasing even in the least in size during that period. — The hermaphrodite forms on which they sit always exceed them very much in size. In most respects except in the total absence of all trace of female organs the males resemble in their anatomy the hermaphrodites on which they sit.

But in the males the nervous system seems to be richer in ganglion cells than in the hermaphrodite. A definite body cavity also seems to be present. It is small in size and lies above the alimentary canal in the position of the so-called uterus of the hermaphrodite (fig. 35, 37). In the males the male genital organs are well developed and generally occupy a considerable portion of the body. In transverse section the testes are seen to fill up all parts of the body not occupied by muscles, alimentary canal and nervous system (figs. 37, 38). These males usually sit on the extreme front of the dorsum of the hermaphrodite, and not as one might expect, and as indeed SEMPER stated, near the female genital aperture. This position they probably take up in order, while being in close connection with the hermaphrodite, to get more food; for there they are nearer the mouth of the *Comatula*. This explanation of their position is indeed the same as that given by Prof. GRAFF, but unlike his explanation it is not given as the reason why they sit on the hermaphrodite form. He thought they were young which were either crowded out from the mouth region of their host or in the cases when only one or two individual *M. glabrum* were parasitic on a *Comatula*, which in leaving its free life had chanced to crawl up the back of one of the individuals already there, and finding it could get plenty of food there it remained. He pictured them with proboscis long extended in order that they might get as much nutriment as possible. But this figure[1] was probably taken from a specimen preserved in alcohol. If so this sufficiently accounts for the extended proboscis, for all *Myzostomidae* killed in alcohol and seawater die with proboscis extended.

These males occur in nearly all cases in which a large hermaphrodite *M. glabrum* occurs solitary on a *Comatula*. Rarely one finds a

[1] l. c. Plate I fig. 11.

male form where two or more hermaphrodites are sitting together on a *Comatula*, and this fact is worthy of notice, for if Prof. GRAFF's explanation were correct, they would occur oftenest, where several *M. glabrum* are parasitic on one Crinoid. Very rarely have I found two males on one hermaphrodite form (fig. 30). The hermaphrodite forms on which the males sit are always large, and contain numerous fully developed ova. In many cases also fully developed spermatozoa, but in some cases the testes are small and not well developed and thus the hermaphrodite becomes physiologically to all intents and purposes female. In these hermaphrodites the vasa deferentia are never absent. Even when the testes in these cases are well developed and contain ripe spermatozoa, they show nothing approximating the number of spermatozoa found in the much smaller males.

I have found these males at all times between November and April. GRAFF thought these so-called Junge occurred oftenest in Trieste in autumn, whether there is any real periodicity in their occurrence is doubtful. — More probably they occur at all times — at any rate in Naples.

The discovery of males with hermaphrodites in this group is not without interest. Their occurrence was known among *Arthropoda* where DARWIN[1] described them as complemental males under the *Cirripedia*, but their origin and meaning remained an enigma to him. It will be interesting before discussing the whole question to examine the results to which DARWIN arrived among the *Cirripedia*.

He found that in the genus *Ibla* the ordinary individuals were not hermaphrodites, but females in whose body sac one or two little worm-like bodies occurred. These proved to be the males of the species examined, *Ibla Cumingii*.

Such a thing had nothing very much unusual in it. But he found in another genus of Cirripedes, *Scalpellum*, these little »complemental males« in much greater numbers, and in this case the individual in which they occurred was hermaphrodite.

In all, four different cases are described by DARWIN as occurring within the limits of the genus *Ibla* and *Scalpellum*.

These are: 1) a female, *Ibla Cumingii*, with a male or rarely two permanently attached to her, protected by her, and nourished by any minute animals which may enter her sack; 2) a female *Scalpellum ornatum* with successive pairs of short-lived males, destitute of mouth

[1] DARWIN, Monograph of the *Cirripedia*. Vol. I.

and stomach, inhabiting two pouches formed on the under side of her valves; 3) hermaphrodites with occasionally one, two or three males, capable of seizing and devouring their prey; 4) and an hermaphrodite *Scalp. vulgare* with »from one or two up to five or six short-lived males without mouth or stomach.«

Lastly we have the ordinary hermaphrodite Cirripedes. Thus we have among the Cirripedes all stages from unisexual forms to complete hermaphrodites.

I shall proceed to show that within the much narrower limits of the genus *Myzostoma*, we have the same passage from the unisexual condition to the hermaphrodite, or if one will vice versâ. My researches had already led me to the conclusions regarding the sexuality of *M. glabrum* detailed in the preceding pages, which conclusions I indeed arrived at about the close of last year 1883, when in January of this year Prof. Graff's most recent paper[1] on the genus arrived in Naples. This short paper contains a description of a number of very interesting new species, 21 in number — among them those collected by the Challenger Expedition. Most of the forms are hermaphrodite, but three forms are especially interesting as being unisexual. These three species are all cysticolous. *M. cysticolum*[2] (Graff) is imperfectly bisexual. The female is 2 mm in diameter, its body cavity is filled with ova and only very scanty rudiments of testes are present, and there are no male sexual apertures. In the small male, which is only 0,8 mm in diameter there are only testes and no traces of female sexual openings. »Im Männchen .... finden sich bloß die beiden compacten Hoden und keine Spur von weiblichen Geschlechtsöffnungen.«

Thus this species is not perfectly unisexual, but when we come to the second and third of the three species we shall find there no traces of male organs in the female, and thus these two species are perfectly unisexual. In *M. inflator* the female is 2,2 mm in length and the male 0,9 mm. Graff[3] says: »Reste von Hoden bei dem Weibchen dieser und der folgenden Species (*M. Murrayi*) nicht constatirt.«

M. Murrayi, the third and last of the three, is very large. The female is 5,5 mm in length, the male 1,3 mm. As stated above this species is perfectly unisexual. Darwin[4] described forms within the *Cirripedia*, which showed all stages from the unisexual state to the

[1] Bulletin of the Museum of Comp. Zoology. No. 7. XXVI. — Graff, Verzeichnis der von den United States Coast Survey steamers »Hassler« und »Blake« von 1867—1879 gesammelten Myzostomiden.

[2] l. c. p. 133. [3] l. c. p. 133. [4] l. c.

hermaphrodite, and here we have the same thing within the much narrower limits of one genus.

It now becomes of importance to endeavour to find out, which is the more primitive condition, hermaphroditism or unisexuality in these particular cases. Most writers[1] on Zoology have simply assumed, that the hermaphroditism of such forms as *Myzostoma* and the *Cirripedia* is the primitive condition. The problem which of the two states is in particular cases the original has been but little attacked.

We are, I think, entitled to assume that among the *Cirripedia* hermaphroditism is secondary. For the lowest Crustaceans are all unisexual, and it is only in such highly modified forms as the *Cirripedia* and *Rhizocephala* that we meet with hermaphroditism. Indeed from a survey of parasites generally one might almost say, that they have a tendency to become hermaphrodite, or that there is a tendency in parasitic life to produce hermaphroditism.

If it be the case that hermaphroditism in *Cirripedia* is secondary then the most primitive of the forms described by Darwin, at least so far as sexuality goes, would be *Ibla Cumingii*, which is unisexual, and possesses males capable of taking in food. The next stage would be *Scalpellum ornatum*, with successive pairs of short-lived males destitute of mouth and stomach. The third *Scalpellum vulgare*, hermaphrodite with from one to six short-lived males without mouth or stomach. Finally if the period between the appearance of two successive generations of short-lived males becomes, to use a mathematical term, infinite, that is if the males entirely disappear, then we get the ordinary hermaphrodite Cirripedes without males such as *Lepas*.

Darwin's case 3 has not been mentioned above. In this case of hermaphrodites with males which have mouth and stomach, the passage is more direct from simple unisexual forms.

And now turning to the *Annelida*, we find there just as we found in the *Crustacea* that the lowest forms are mostly unisexual. Only in highly modified forms[2] such as the leeches, and *Oligochaeta* and the parasitic genus *Myzostoma* do we find hermaphroditism.

My own view is that primitively all the segments of an Annelid produce either ova or spermatozoa. Later some of the segments may lose all sexual function while in others, by a gradually acquired ten-

[1] Comp. Huxley, Anatomy of Invertebrated Animals. 1877. p. 67, and Claus, Grundzüge der Zoologie.

[2] Unfortunately two species of *Polygordius* are hermaphrodite, while one is unisexual.

dency towards hermaphroditism, the embryonic sexual cells of one or more segments may become spermatozoa instead of ova, or vice versâ.

Again it should not be forgotten that most hermaphrodites have very complicated sexual ducts etc., which are obviously not primitive organs but adaptations designed in most cases to bring about cross fertilisation and prevent self-impregnation. Such ducts could only arise in pretty highly developed forms, that is to say could only be converted to secondary sexual uses in cases in which they really were present beforehand, and hence only in pretty highly developed forms. This circumstance points rather to a developing hermaphroditism which arose pari passu with the conversion of these ducts to sexual uses, for otherwise self-impregnation would usually occur.

Certain recent researches seem to favour the view of the probable origin of hermaphroditism from the conversion of the parts of the sexual cells of one sex to sexual elements of the other. Many points of great interest are concerned in SPENGEL's critique[1] of two papers, one by BOURNE[2], the other by MARSHALL[3], and in an earlier work of SPENGEL's[4]. SPENGEL in this review declares his conviction that the so-called BIDDER's organ of the Amphibia cannot be regarded as the rudiment of a female sexual organ, whatever else it may be, for it is present in both sexes, and that when a real hermaphroditism occurs among Amphibia BIDDER's organ is not concerned in its formation, but that such hermaphroditism is brought about by the transformation (Umwandlung) to ovary of part of the tissue which in a normal individual forms testes, and that in this ovary so produced the ova attain their normal size and pigment.

BOURNE describes a specimen of *R. temporaria*, which on the right side possesses a well developed ovary, while on the left the anterior end of the ovary encloses an irregular testis not sharply marked off from the ovarial tissue.

MARSHALL describes an individual (*B*) which macroscopically

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[1] SPENGEL, Zwitterbildungen bei Amphibien. Biol. Centralblatt. Bd. IV. Nr. 8. p. 235—241.

[2] A. G. BOURNE, On certain abnormalities in the Common Frog. 1. The occurrence of an ovotestis. Quart. Journ. Microsc. Sci. Vol. 24. p. 83—86. Pl. IV.

[3] A. M. MARSHALL, On certain abnormal conditions of the reproductive organs of the common frog. Journ. of Anat. and Physiol. Vol. 18. p. 121—144. Pl. VI—VII.

[4] SPENGEL, Arbeiten aus dem Zool.-Zoot. Inst. zu Würzburg. Bd. III. 1876.

seems to be a male, but at the anterior end of the right testis there is a pigmented fold which possesses a number of button-like processes, and on microscopic examination it is seen that these processes are ova, which there lie close to the surface, and are further scattered between the lobules throughout the whole testis. The Müllerian duct is also very well developed.

He found in another individual (*D*) an ovary on the left side with normal eggs, which however show in great part traces of degeneration. On the right side the sexual organ has chiefly the characters of a testis. The sexual ducts are those of a female.

Thus it is seen that in the Amphibia hermaphroditism is brought about by the conversion in some individual of part of its male sexual cells into ova, or of its female cells, if it be a female into spermatozoa, and is not really due to the rudiment of a hermaphrodite state present in all individuals. Further the so-called rudimentary ovary is not concerned in the production of hermaphroditism.

Some interesting researches have recently been published by von Brunn [1] on the spermatozoa of *Paludina vivipara*. In this paper the author explains the origin of the worm-like spermatozoa by the hypothesis [2], that there is a tendency in the sexual characters of the male organs of *Paludina vivipara* to produce female characters, and compares very justly the structure of the testis of *Paludina* to the hermaphrodite gland of the *Pulmonata*. He points out that the worm-like spermatozoa occupy the same position in the testes of *Paludina* as the ova in the hermaphrodite gland of *Pulmonata*. He further considers [3] the Pulmonate hermaphrodite gland to be derived from a simpler unisexual state [4].

From all this I think we may gather that at any rate in very many cases hermaphroditism is a secondary condition brought about in the males or females, or in both, of unisexual animals, either by some innate tendency to it or by something in the conditions of existence of the particular species.

It was pointed out further back that among *Crustacea* and *Anne-*

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[1] Max v. Brunn, Untersuch. über die doppelte Form d. Samenkörper von *Paludina vivipara*. Archiv f. Mikrosk. Anat. Bd. 23. Heft 4.

[2] »Weibliche Tendenz im Hoden.«

[3] l. c. Physiologischer Theil. p. 478.

[4] It is worthy of remark that one often finds in the vesiculae seminales of the male of *M. glabrum*, not small quantities of undeveloped spermatozoa. One might perhaps here in the male assume the existence of a »weibliche Tendenz im Hoden«.

lida the unisexual state occurs in nearly all cases, including nearly all the lowest forms, and I think we are now entitled to assume that the more primitive and original state in the genus *Myzostoma* is the unisexual.

And now we are in a position to trace out the development of, and get some clue to the meaning of hermaphroditism in the *Myzostomidae*.

It is obvious that the starting point of the series is the unisexual form such as *M. inflator* or *M. Murrayi*. The next stage in the process is imperfect hermaphroditism with fully developed males. — A hermaphroditism in which male organs are beginning to be developed but are not yet functional. This is seen in *M. cysticolum*. The European *M. glabrum* gives us further development, there we have hermaphrodites with both male and female organs fully developed and functional, but still with males, the males however only in small numbers, and then only when perfect or imperfect hermaphrodites sit singly on a *Comatula*, the forms which possess no males living in groups of two, three, or more, and probably reciprocally hermaphrodite. Lastly, we probably possess in some of the remaining species of the genus perfect hermaphrodites without males, the males having become extinct. This is probably the case in *M. cirriferum*, which usually forms a small colony of several individuals on each *Comatula mediterranea*.

So far as is known the remaining species of *Myzostoma* are hermaphrodite and have no males. It must however be borne in mind that males may and probably will be found in some cases at any rate.

It may be useful and interesting to tabulate the results obtained in the *Cirripedia* and in *Myzostoma*.

Cirripedia.

Ibla Cumingii	unisexual, males possess stomach.
Scalpellum ornatum	unisexual, males without stomach.
Scalpellum vulgare	hermaphrodite with males, males without stomach and quite degenerate.
Ibla quadrivalvis and most species of *Cirripedia*	hermaphrodite without males.

Myzostomidae.

M. inflata, *M. Murrayi*	perfectly unisexual.
M. cysticolum	unisexual with rudiments of hermaphroditism.
M. glabrum	hermaphrodite with males.
M. cirriferum and other species of *Myzostoma*	hermaphrodite without males.

If the genus *Myzostoma* was once unisexual, what has brought about the change to Hermaphroditism? The answer is probably the following. The necessity of it for the continued existence of some species of the genus. The eggs are very small, and hatch a minute free swimming larva, which has to trust very much to chance to find a future host. Only by the development of a vast number of eggs, and the provision of efficient means for the fertilisation of those eggs is the continued existence of some species of the genus rendered a possibility.

The first condition, the development of a vast number of eggs, is realized to an astonishing degree. One has only to examine a full grown specimen of *M. glabrum* or *M. cirriferum* to assure himself of this. I have often been astonished at the enormous number of eggs contained in one *M. glabrum*. When we consider too that this production of eggs is a continous one extending over at least some months, and that eggs are probably laid daily, it is evident that each individual in its lifetime produces vast numbers of eggs. But the production of eggs is not the only factor. — They must be fertilised. The difficulty of the continued existence of the species is increased by this fact. For if the chances of one larva finding a host are exceedingly small, the chances of two larvae, which when adult will be male and female respectively, coming to occupy the same host must be much smaller. And in many cases only two or more females would get to one host. This latter state of things would become much more intensified if for any reason the number of males produced from the young larvae should in some way or other become diminished. Hence it becomes of advantage to complement the small males by the development in the female of testes, from part of the female organs as in Amphibia. It may well be that at first the testes only become functional in particular cases in which females alone without males occupied a particular *Comatula*. In time the progress to complete hermaphroditism becomes more and more pronounced, and finally in some cases the males become lost.

This extinction[1] of the males may be brought about by a diminution in their size and a corresponding increase in size and number of hermaphrodites, which devote themselves to the production of eggs and sper-

[1] This extinction of the males might be brought about by a periodicity in their occurrence arising. If the periodicity got more and more lengthened, it would in the end become so to speak infinite, and the males would disappear. Compare Weismann, Über die Entstehung der cyclischen Fortpflanzung bei den Daphnoiden. Abdruck aus d. Zeitschr. für wiss. Zoologie, 27.—33. Bd. Here such a periodicity is associated with a somewhat different result, viz. Parthogenesis.

matozoa, and thus the number of young arising from the union of hermaphrodites, when hermaphrodites are once formed, will greatly increase and probably in the end crowd out of existence the young produced by the union of males with hermaphrodites.

Thus as the result the following conclusions may be drawn.

The term complemental male adopted by the great naturalist is probably not an expression of the true morphological meaning of the phenomenon, physiologically it may be correct. Morphologically it is rather the male organs of the hermaphrodite, which are complemental to those of the male. The males are really primitive, and refer us back to a time when the parent stock was unisexual.

Hermaphroditism, probably all hermaphroditism, had its origin in a unisexual condition. It has been gradually acquired, in some cases perhaps as the result of a tendency in the sexual organs towards hermaphroditism, in others in order to provide for the continued existence of the form. In some cases it is the females, which have become hermaphrodite as, for example, *Myzostoma*, in others it is probably the males, in others still both males and females. In those cases where only one sex has become hermaphrodite, the other sex has probably in most cases become either periodic in its appearance if male, or else extinct.

The foregoing researches were in great part carried out at the Zoological Station of Naples. On the recommendation of Prof. SEMPER, to whom my best thanks are due, the Senate of the University of Würzburg approved my application for the Bavarian table at Naples during several of the winter months. But as the contract for the table was in October last not yet renewed, I journeyed to Naples without the nomination of the Bavarian government. Prof. DOHRN however very kindly received me and gave me a place in the Station, where I worked from November till the middle of April. For this and many other acts of kindness I beg to tender him my best thanks.

I should like further to express my thanks to the staff of the Station and more especially to Drs. PAUL MAYER, EISIG, BRANDT and to the Conservator Sig. SALVATORE LO BIANCO.

Freiburg i. B., July 17th 1884.

Printed by Breitkopf and Härtel, Leipzig.